OBSERVATIONS ON THE NUTRITION OF THE LAND PLANARIAN ORTHODEMUS TERRESTRIS (O. F. MÜLLER)[1]

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The Turbellaria as a class are carnivorous and previous investigations have shown that the range of prey available to these relatively simple animals has been greatly increased through the development of efficient feeding mechanisms in the form of progressive elaborations in the structure and use of the pharynx (Jennings, 1957). The Tricladida in particular, with the protrusible cylindrical type of plicate pharynx, are active and successful predators and the nutrition of the aquatic forms has already received much attention (Willier, Hyman and Rifenburgh, 1925; Kelley, 1931; Jennings, 1957). Little is known, however, of feeding and digestion in those triclads of terrestrial habit and hence a representative of this group, *Orthodemus terrestris* (O. F. Müller), has been examined to gain some measure of the influence of a land existence upon the typical pattern of triclad nutrition.

Materials and Methods

Orthodemus terrestris occurs beneath limestone debris and fallen branches in the Fairburn, Malham and Settle districts of Yorkshire. Specimens collected throughout the year were presented in the laboratory with representatives of the fauna associated with them under natural conditions, and their food preferences and methods of capture and ingestion of the selected prey observed. The course of digestion was traced by histological examination of series of individuals previously starved to clear the gut and then killed at progressive intervals after being fed on either the natural food or test foods such as frog blood and boiled starch paste. After fixation in Susa at 30° C. sections were cut at 8 μ and stained with haematoxylin and eosin, Feulgen, benzidine, periodic acid-Schiff, Alcian blue and Lugol's iodine. Food reserves were studied after fixation in Flemming (for fat) and 90% alcohol containing 1% picric acid (for carbohydrates and proteins), sections of specimens fixed in the latter reagent being stained by the Best's carmine, P.A.S. and modified Millon methods.

Observations

The food and feeding methods

Orthodemus feeds mainly upon slugs (*Arion* sp.) and small earthworms. It will also attack small arthropods such as collembola, wood-lice, insect larvae and myriapods if these are injured or incapacitated in any way but normally they are too active for capture by the flatworm, which lacks any trapping or snaring

[1] New combination by Hyman (1954).

devices. The mucus produced during locomotion quickly dries out and plays no part in the capture of food, unlike that of some aquatic triclads which persists about the habitat as sticky strands to entangle insect larvae and crustaceans. The prey appears to be found by chance and starved individuals show no awareness of the proximity of either damaged or intact animals until random movements bring them into direct contact.

When an appropriately sized slug or earthworm is encountered the flatworm rapidly extends across the width of the prey until it can grip the substratum on each side and so pin the captured animal beneath the arched body. The grip on both prey and substratum is helped by copious secretions of mucus from the ventral surface and is so effective that prey rarely escape. Movement across the prey continues until the mouth, which lies ventrally approximately one-third of the body length from the posterior end, can be brought into contact with it. The muscular tubular pharynx is then protruded through the mouth and after moving rapidly over the surface of the prey is eventually thrust through the body wall (Fig. 1). When this occurs the flatworm changes position slightly to bring the mouth directly over the point of penetration to enable the pharynx to extend as fully as possible into the prey. The precise means of penetration could not be

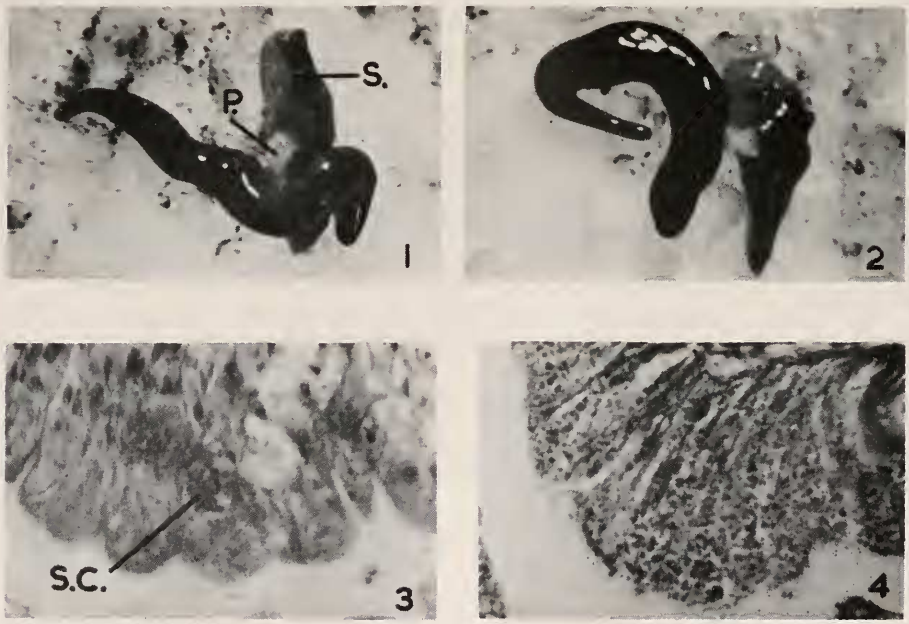

FIGURE 1. *Orthodemus* attacking a slug (S). The protruded pharynx (P) is penetrating the integument of the slug to withdraw the body contents. Magnification × 5.

FIGURE 2. Photographed 15 minutes after Figure 1. Feeding is complete and the flatworm is retracting the pharynx from the remnants of the slug. Magnification as in Figure 1.

FIGURE 3. A portion of the gastrodermis in *Orthodemus* showing a "sphere-cell" (S.C) surrounded by columnar cells. Haematoxylin and eosin. Scale: 1 cm. = 20 μ.

FIGURE 4. Gastrodermis of *Orthodemus*, 4 hours after a meal of starch paste, showing columnar cells loaded with phagocytosed material. Periodic acid-Schiff. Scale as in Figure 3.

ascertained, but it would appear to be purely mechanical, with the pharynx merely forcing its way inwards through the epidermis and musculature. Complete penetration is achieved within 30–60 seconds of first contact and there is no evidence to suggest the process is assisted by either regurgitation of solvent juices or the selection of external openings.

Once within the body cavity the pharynx moves around disorganzing the softer tissues to pass them back in a finely divided condition into the gut. The disruption of the tissues is rapid, and, like the penetration of the body wall, is mechanical with the pharynx acting as a simple suctorial tube extracting tissue fragments and body fluids. Withdrawal of the body contents continues until either only the collapsed and empty body wall is left, or the flatworm is replete, when the pharynx is retracted and the remnants of the prey abandoned (Fig. 2). Feeding lasts 10–20 minutes and during this period the flatworm lies in a very characteristic position across the prey, with the head region often raised and swinging slowly from side to side. In the early stages the food may be abandoned if the flatworm is disturbed or the incident light increased but later, when the pharynx is inserted and ingestion proceeding, the feeding individual is less susceptible to external stimuli and in the laboratory can often be manoeuvered into situations more suited to observation.

The laboratory stock of *Orthodemus* was sexually mature and produced cocoons between April and August. Up to six young, 3–4 mm. long, emerged from each cocoon within three weeks of laying and these fed in the same manner as the adults upon newly hatched or very young slugs. The latter were common in the habitat during the flatworm's breeding season and appear to form the staple diet of young *Orthodemus*, for isolated mucus cells and granules of a black pigment similar to that of the slug were often found amongst the gut contents of the young individuals fixed immediately after collection.

The structure of the gut and the course of digestion

The gut in *Orthodemus* has the typical triclad arrangement with numerous lateral caeca arising from each of the three main branches. The pharynx is of the cylindrical plicate type, and can be protruded through the mouth by simple muscular elongation.

The gastrodermis (Figs. 3 and 4) consists of a single layer of non-ciliated cells standing on a delicate basement membrane. Two types of cell occur. The larger and more numerous are columnar, 40–50 μ in height, with basal eosinophilous inclusions which apparently represent phagocytosed food particles, for they disappear rapidly during starvation. The second type is spherical or slightly pear-shaped, 25–30 μ high, and situated between the bases of the columnar cells in the ratio of approximately one to every ten of the latter. They contain eight to twelve proteinaceous spheres which stain heavily with haematoxylin and modified Millon method and disappear only slowly with starvation. These "sphere-cells" appear, therefore, to function as sites of protein storage—a conclusion supported by the absence of changes in appearance or staining reaction which can be correlated with digestive processes.

The presence of discrete particles within the columnar gut cells indicated that digestion in *Orthodemus* is intracellular and this was confirmed by an examination

of individuals fixed at various intervals after observed feeds on slugs. Immediately after feeding the gut lumen is filled with a heterogeneous mass of cells, nuclei and muscle fragments already of suitable size for phagocytosis through the extreme disruption caused by the pharynx during ingestion. Phagocytosis begins as the first tissue fragments enter the gut and within fifteen minutes engulfed particles are found throughout the gastrodermis. They are contained at first in small vacuoles near the free distal border of the columnar cells, and phagocytosed muscle fragments and nuclei are clearly recognizable. With time, however, the fragments lose their identity and condense to homogeneous spheres which pass back deeper into the cells to disappear as digestion and absorption proceed. Four hours after feeding the columnar cells are loaded with phagocytosed material and they show a considerable increase in volume, with their walls becoming indistinct and the whole gastrodermis appearing almost syncytial. Complete digestion of a meal takes 12–24 hours, depending upon the amount of food taken, but any particles too big for phagocytosis, such as occasional large muscle fragments, are unaffected and remain unchanged in the gut lumen.

Experimental demonstration of the complete absence of intraluminar digestion was obtained by feeding frog blood and boiled starch paste. The former was readily taken by the flatworms but the starch appeared to be less palatable and had to be injected into a boiled portion of earthworm to ensure its ingestion. Fixation after blood feeding showed that many erythrocytes were ruptured during their passage through the pharynx, demonstrating its effective triturating action, and the corpuscle fragments, nuclei, and intact erythrocytes were quickly phagocytosed by the gut cells. Staining with the Feulgen and benzidine techniques showed progressive breakdown and disappearance of phagocytosed nuclei and haemoglobin, but in sharp contrast material in the lumen remained unchanged in appearance and staining capacity until it was either taken up by the cells or eventually expelled from the gut eight to twelve hours after feeding. Similar results were obtained after feeding with starch paste; staining with Lugol and P.A.S. showed digestion and absorption of starch within the columnar cells (Fig. 4), whilst that remaining in the lumen was quite unaltered.

It was not possible to determine the pH conditions of intracellular digestion owing to the limited number of specimens and the difficulty of administering food containing indicators.

The food reserves

Fat forms the principal food reserve in *Orthodemus* and the bulk is stored in the mesenchyme as large globules 15–20 μ in diameter, whilst smaller amounts are scattered as droplets 3–4 μ in diameter in the columnar cells of the gastrodermis.

As already stated, protein reserves are found within the so-called "sphere-cells" of the gastrodermis (Fig. 3) and in adult *Orthodemus* these show a marked seasonal variation. Thus in early spring the gastrodermis contains more "sphere-cells," each with large, dense and heavily staining spheres, but during the summer months when the gonads are mature and the flatworms producing cocoons the number of cells decreases and the spheres of those remaining shrink and stain only lightly. In the late summer, however, the cells start to increase in number and reach a maximum of one to every ten of the columnar cells by October or November.

Thus there is a build-up of reserve protein during the late summer which is rapidly depleted in the following breeding season.

There are no significant amounts of carbohydrate reserves. Staining with Best's carmine and P.A.S. reveals only very small amounts of glycogen which occur as tiny irregular granules scattered through the mesenchyme and columnar gut cells.

Discussion

It is evident from these observations that nutrition in *Orthodemus terrestris* differs very little from that described in the related aquatic triclads (Willier, Hyman and Rifenburgh, 1925; Kelley, 1931; Jennings, 1957). The typical triclad feeding mechanism, with the pharynx functioning as a suctorial tube which penetrates the prey to withdraw the body contents piecemeal, has apparently proved adequate to the needs of a terrestrial life and is retained unmodified. It allows the flatworm to deal effectively with slugs or earthworms which in the absence of devices for trapping more active animals appear to form the bulk of the diet. The failure of the mucous locomotory trail to persist and perform the secondary function of ensnaring the prey, as it does in aquatic triclads, is due perhaps to the terrestrial environment which although damp and humid does not prevent desiccation of the trail soon after its formation.

The retention of suctorial feeding, with extreme disruption of the food during ingestion, allows phagocytosis by the columnar cells to begin immediately food enters the gut. Consequently there has been no stimulus for the development of intraluminar digestion and the primitive condition of exclusively intracellular breakdown persists, exactly as in the aquatic triclads. A further similarity between the latter and *Orthodemus* is seen in the form and location of the food reserves, and particularly of protein stored in both cases in special "sphere-cells" in the gastrodermis.

It would appear, therefore, that the adoption of the terrestrial habit by *Orthodemus* has not necessitated any fundamental modification of the basic triclad methods of feeding and digestion. This is probably true of most other terrestrial triclads, for of the few existing accounts which mention nutrition, almost all describe or infer suctorial feeding upon earthworms, slugs and occasionally other invertebrates (Percival, 1925; Eastham, 1933; Johri, 1952; Froehlich, 1955; Pfitzner, 1958), and since this has such a profound effect upon the particle size of food entering the gut it is likely that it permits retention of purely intracellular digestion, as in *Orthodemus*. A few South American species, however, are reported to swallow their food whole (Froehlich, 1955) so that in these cases, unless preliminary breakup within the gut is achieved mechanically as in some rhabdocoels (Jennings, 1957), at least some degree of intraluminar digestion must occur.

I wish to thank Professor E. A. Spaul for his advice and encouragement during the course of this work.

Summary

1. The land planarian *Orthodemus terrestris* feeds principally upon small slugs and earthworms which are captured after chance encounter.

2. The typical triclad method of feeding, with the protruded cylindrical plicate

pharynx inserted into the prey to disrupt and withdraw the body contents, is used without modification.

3. Disintegration of the food during ingestion is so effective that the resultant particles are available for immediate phagocytosis by the gut cells and intraluminar digestion is absent.

4. The food reserves consist of fat stored in the mesenchyme and columnar gut cells, and protein stored in gastrodermal "sphere-cells." Protein reserves are depleted during the breeding season and replenished in the late summer and autumn.

5. It would appear that the basic triclad methods of feeding and digestive processes are quite adequate to the needs of terrestrial life and *Orthodemus* shows no particular adaptation to this so far as nutrition is concerned.

LITERATURE CITED

Eastham, L. E. S., 1933. Morphological notes on the terrestrial triclad *Rhynchodemus brittanicus* Percival. *Proc. Zool. Soc. Lond.*, **1933**: 889–895.

Froehlich, C. G., 1955. On the biology of land planarians. *Bol. Fac. Filos., Cienc. Letr., Univ. São Paulo, Zoologia,* **20**: 263–272.

Hyman, L. H., 1954. Some land planarians of the United States and Europe, with remarks on nomenclature. *Amer. Mus. Novitates,* no. 1667, 21 pp.

Jennings, J. B., 1957. Studies on feeding, digestion and food storage in free-living flatworms (Platyhelminthes: Turbellaria). *Biol. Bull.,* **112**: 63–80.

Johri, L. N., 1952. A report on a Turbellarian *Placocephalus kewense,* from Delhi State, and its feeding behaviour on the live earthworm *Pheretima posthuma. Sci-Cult.,* **18**: No. 6, 291.

Kelley, E. G., 1931. The intra-cellular digestion of thymus nucleo-protein in triclad flatworms. *Physiol. Zoöl.,* **4**: 515–541.

Percival, E., 1925. *Rhynchodemus brittanicus,* n. sp. A new British terrestrial triclad, with a note on the excretion of calcium carbonate. *Quart. J. Micro. Sci.,* **69**: 344–355.

Pfitzner, I., 1958. Die Bedingungen der Fortbewegung bei den deutschen Landplanarien. *Zool. Beitr., Berl.,* **3**: 235–310.

Willier, B. H., L. H. Hyman and S. A. Rifenburgh, 1925. A histochemical study of intracellular digestion in triclad flatworms. *J. Morph.,* **40**: 299–340.